

# Vestigial Ophiopluteal Structures in the Lecithotrophic Larvae of *Ophionereis schayeri* (Ophiuroidea)

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**Abstract.** Evolution of echinoderm development from a feeding to a non-feeding mode can be examined by studying non-feeding larvae with structures that appear to be vestiges derived from a feeding ancestral state. The lecithotrophic larvae of the Australian brittle star *Ophionereis schayeri* possess such features, and the early development of this species was documented by light and scanning electron microscopy. The embryos undergo irregular cleavage, resulting in the formation of different sized blastomeres, with subsequent development through a wrinkled blastula stage. The lecithotrophic larva of *O. schayeri* possesses several vestigial ophiopluteal structures, including a continuous ciliated band, a larval gut, and a larval skeleton. The ciliated band is a reduced expression of the continuous ciliated band typical of ophioplutei. The larval gut is a transiently complete system, but an esophageal plug and rapid closure of the blastopore renders it nonfunctional. The larval skeleton, though reduced, consists of four rods corresponding to the body, posterolateral, anterolateral, and postoral rods characteristic of an ophiopluteus. Due to a heterochrony in larval skeletogenesis, the postoral rods develop early and simultaneously with the other rods. Compared with the larvae of other lecithotrophic ophiuroids, the larva of *O. schayeri* is one of the most reduced ophiopluteal forms reported to date.

## Introduction

The diversity of developmental modes in marine invertebrates has intrigued investigators for many years (Wray, 1995). This diversity is presumed to be associated with life history evolution, but the direction of the evolutionary change, whether from planktotrophy to lecithotrophy or *vice versa*, has been a topic of debate. Phylogenetic analyses of

larval morphological traits have been combined with molecular characters to produce a better understanding of the evolution of different life histories (Wray, 1996; Hart *et al.*, 1997; McHugh and Rouse, 1998). For echinoderms, planktotrophy is considered to be a plesiomorphic character. The loss of complex larval feeding structures in the evolution of non-feeding development involves major alterations in larval morphology, which are thought to be irreversible (Strathmann, 1974). Thus, the occurrence of ophiuroid and echinoid larvae with vestigial larval feeding structures (*e.g.*, pluteal arms, skeleton, ciliated band) indicates that they have evolved from an ancestral form that had a feeding larva. The transition from planktotrophy to lecithotrophy is predicted to be reversible, however, when maternal nutritional investment is altered due to selective pressures, without a resulting change in larval morphology (McEdward and Janies, 1997).

Planktotrophic development in ophiuroids occurs through an 8-armed ophiopluteus (Table 1). Lecithotrophic development in ophiuroids is associated with a range of larval forms—including planktonic ophioplutei with a reduced number of arms, vitellaria larvae, and benthic and brooded larval forms—that may or may not possess ophiopluteal features (Table 1). Thus far, eleven ophiuroid species are known to have lecithotrophic larvae with vestigial larval structures, seven with planktonic development, one with benthic development, and three with brooded development (Table 1). This list suggests that lecithotrophic species with developmental features intermediate between planktotrophy and lecithotrophy are uncommon. This may be due to evolutionary instability of intermediate larval forms (Vance, 1973) or may reflect inadequate sampling. Further examination of ophiuroids with lecithotrophic larvae and comparison of development in closely related species is needed to determine the processes and pathways underlying the loss of superfluous larval structures during the evolution of lecithotrophy.

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Table 1

*Developmental modes in the Ophiuroidea, with emphasis on lecithotrophic species that retain larval feeding structures*

Developmental mode	Larval form	Species	Reference	
Planktotrophic	8-arm ophiopluteus	>50 species	MacBride, 1907; Mortensen, 1921; Narasimhamurti, 1933; Olsen, 1942; Hendler, 1975; Mladenov, 1985; Yamashita, 1985; Hendler, 1991	
Lecithotrophic (planktonic)	Reduced ophiopluteus			
	6 arms	<i>Amphiura filiformis</i>	Fell, 1945	
	2 arms	<i>Ophiura affinis</i> , <i>Amphiura chiajei</i> , <i>Ophiothrix oerstedii</i>	Fell, 1945; Fenaux, 1963; Mladenov, 1979	
	Armless	<i>Ophiopluteus claparedei</i>	Fell, 1945	
	Vitellaria (with larval structures)	<i>Ophiolepis cincta</i> , <i>Ophionereis annulata</i>	Mortensen, 1938; *Hendler, 1982	
Lecithotrophic (benthic)	Vitellaria (no larval structures)	<i>Ophiura brevispina</i> , <i>Ophionereis squamulosa</i> , <i>Ophioderma longicauda</i> , <i>Ophiolepis elegans</i> , <i>Ophiolpocus japonicus</i>	Grave, 1900; *Mortensen, 1921; Fenaux, 1969; Stancyk, 1973; Komatsu and Shoshaku, 1993	
	(With larval structures)	<i>Amphioplus abditus</i>	Hendler, 1978	
	(No larval structures)	Kirk's ophiuroid	Fell, 1941	
	Lecithotrophic (brooded)	(With larval structures)	<i>Amphipholis japonica</i> , <i>Amphipholis squamata</i> , <i>Ophiontus hexactis</i>	Murakami, 1940; Fell, 1946; Mortensen, 1921
		(No larval structures)	<i>Ophionereis olivacea</i> , <i>Ophionereis vivipara</i> , and >68 other species	*Byrne, 1991; Hendler, 1991; *Mortensen, 1933

\* Previous studies on *Ophionereis* species.

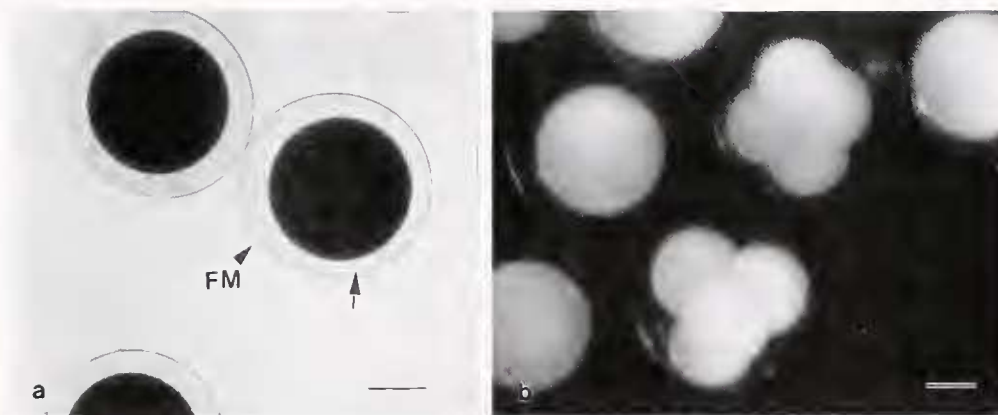
The Australian ophiuroid *Ophionereis schayeri* develops through a lecithotrophic larva that retains a suite of larval feeding structures. It spawns 241  $\mu\text{m}$  diameter, lipid-rich eggs and completes development in 6–7 days (Moloney and Byrne, 1994; Selvakumaraswamy and Byrne, 1995; Selvakumaraswamy and Byrne, 1998, 1999). The development of four other lecithotrophic *Ophionereis* species has been described, with two species possessing some pluteal features and the other two completely lacking them (Table 1). The selective pressures underlying the developmental diversity in ophiuroids are unknown, and the larval forms in these *Ophionereis* species are compared here to provide insights on how loss of larval structures may have occurred within this clade. In this study the early larvae of *O. schayeri* are described, with emphasis on the development of its vestigial ophiopluteal structures.

### Materials and Methods

*Ophionereis schayeri* was collected from several sites in New South Wales during its summer spawning season, from January to April, in 1996 and 1997. Animals were induced to spawn by combined light and temperature shock. About 20 individuals were transferred repeatedly between seawater at 34 C and at ambient temperature (19–23 C), then

kept in the dark for half an hour. This was repeated every half hour for 2–3 h. For larval culture, fertilized eggs were rinsed three times in filtered seawater (1  $\mu\text{m}$ ), placed into 500-ml beakers at densities of 5 eggs/ml, and kept constantly stirred at ambient temperatures (19°–23°C). The seawater was changed every second day by aspiration through an 80- $\mu\text{m}$  mesh.

The larval skeleton was visualized as follows. Embryos and larvae were fixed for 1 h in 2% paraformaldehyde buffered in 0.2- $\mu\text{m}$  filtered seawater, and then stored in 70% ethanol. They were then made translucent by dehydration and clearing in a 1:1 solution of benzyl benzoate and benzyl alcohol, according to Amemiya and Emler (1992). The cleared larvae were examined with cross polarized light. For scanning electron microscopy (SEM) and light microscopy (LM), embryos and larvae were fixed for 1 h in 2.5% glutaraldehyde, buffered in 0.2- $\mu\text{m}$  filtered seawater, rinsed in 2.5% sodium hydrogen carbonate, postfixed for 1 h in 2% osmium tetroxide buffered in 2.5% sodium hydrogen carbonate, rinsed in distilled water, and dehydrated. Specimens for SEM were then critically point dried, coated with 20 nm of gold, and examined with a JEOL 35C scanning electron microscope set at 15 kv. Specimens for resin embedding and (LM) serial sectioning were further dehydrated, infiltrated,



**Figure 1.** Fertilization and cleavage of *Ophioneis schayeri*. (a) Fertilized eggs have a raised fertilization membrane (FM) and large perivitelline space (arrow). (b) Fertilized eggs and four-cell embryos. Scale bars = 100  $\mu\text{m}$ .

and embedded in Spurr's resin at 80°C for 20 h. Larvae were serial sectioned at 0.9  $\mu\text{m}$  and stained with 1% toluidine blue in 0.5% ethanolamine.

## Results

### Early development

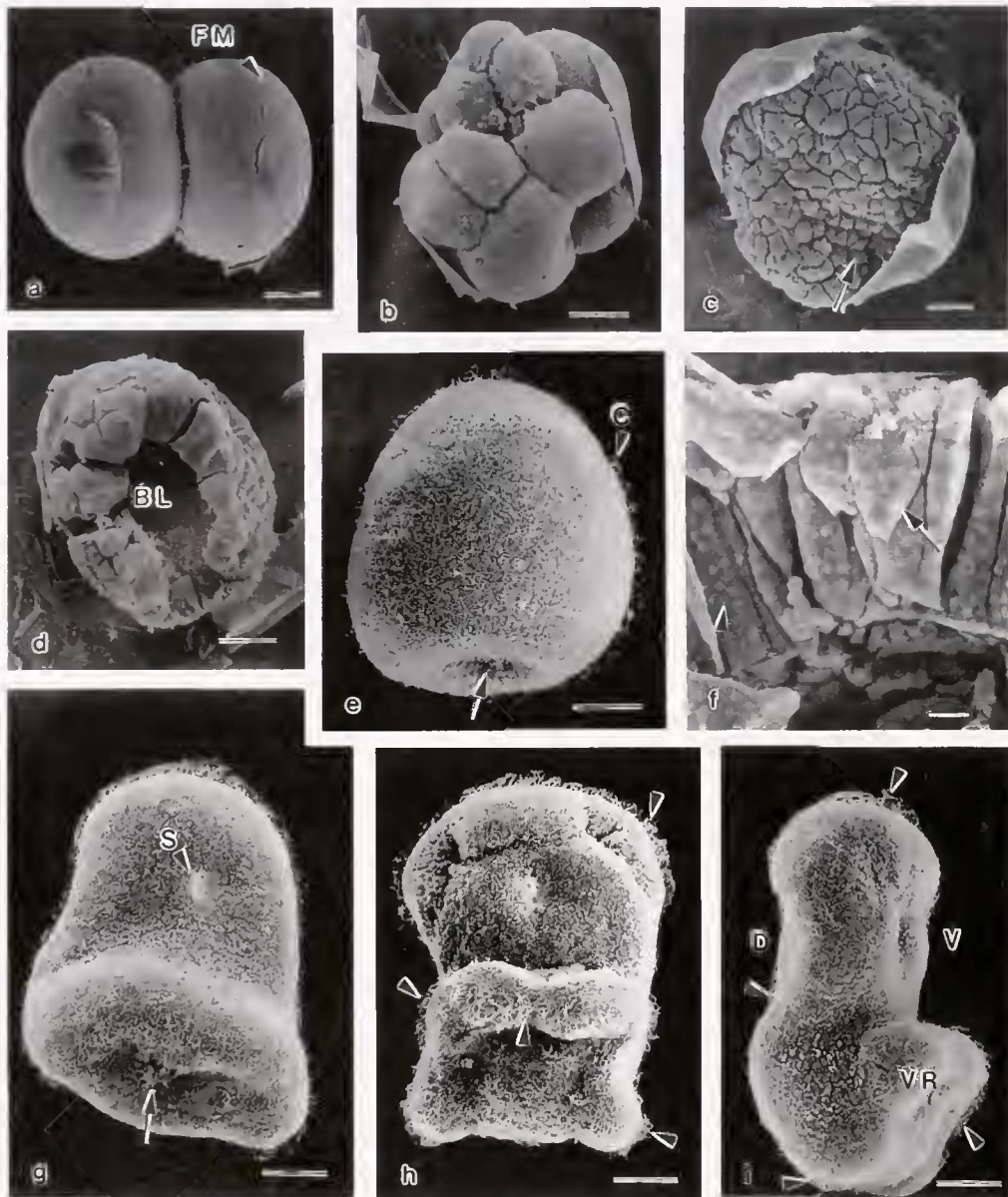
Fertilized eggs had a 50- $\mu\text{m}$ -wide perivitelline space between the oolemma and the fertilization envelope (Fig. 1a, b). Although looked for, polar bodies were never observed, indicating that meiosis is completed during ovulation and spawning. Cleavage was initially equal and radial (Fig. 2a). After second cleavage, however, the division planes became offset, resulting in an irregular arrangement of the blastomeres (Fig. 2b). Beyond third cleavage, cell division became asynchronous, with some cells cleaving before others (Fig. 2b). The irregular arrangement of blastomeres remained evident to the blastula stage. About 12 h after fertilization, the embryos took on a slightly contorted shape as they developed into wrinkled blastulae. The wrinkles were shallow, forming slight indentations in the epithelium (Fig. 2c). The blastulae subsequently smoothed (Fig. 2d), the epithelium became uniformly ciliated, and the embryos started to rotate within the fertilization envelope. The blastulae hatched about 16 h after fertilization and swam with their anterior pole forward, in no particular direction or orientation. Gastrulation occurred about 21 h after fertilization by invagination of the vegetal plate (Fig. 2e). During gastrulation, the epithelial cells changed shape from cuboidal (Fig. 2d) to columnar (Fig. 2f). Round cells in the epithelium, which were situated towards the apical surface, may be recently divided cells (Fig. 2f). Lipid droplets in the eggs of *O. schayeri* were about 3  $\mu\text{m}$  in diameter (Moloney and Byrne, 1994) and were conspicuous in the epithelial cells of gastrulae (Fig. 2f).

### Formation of a reduced ophiopluteus

**Larval gut.** Twenty-five hours after fertilization the gastrulae elongated, and the blastopore started to close (Figs. 2g, 3c). An anterior ventral depression marking the position of the stomodeal invagination was also evident (Figs. 2g, 3a), but this opening was much smaller than the mouth of typical ophioplutei. Larvae sectioned at this stage had a digestive tract with an incomplete lumen; the esophagus was open to the exterior *via* the stomodeum, but its connection to the stomach was blocked by what appeared to be an esophageal plug (Fig. 3a, b). The larval gut was filled with mesenchyme cells, and opened posteriorly *via* the blastopore (Fig. 3c). Closure of the blastopore after 25 h, however, resulted in formation of a larval gut that was only transiently complete, and thus the larvae did not feed. Subsequently, the gut became a simple sac.

**Ciliated band.** After 36 h and further elongation, a distinct ventral ridge appeared near the posterior end of the larva, and the ciliated band subsequently formed along this structure (Fig. 2g). Formation of the ventral ridge transformed the late gastrula into an early larva that was bilaterally symmetrical through the anterior-posterior axis (Fig. 2g).

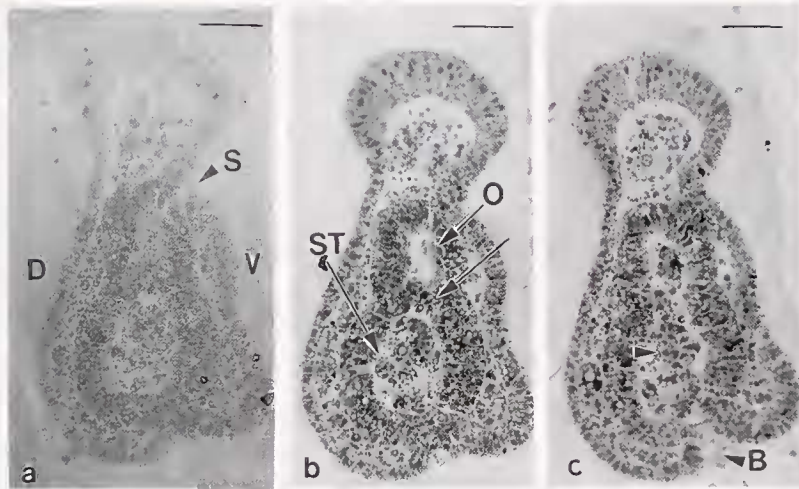
The larva (335  $\mu\text{m}$  in length) developed a single continuous ciliated band about 42 h after fertilization (Fig. 2h, i). The ciliated band ran from the anterior to the posterior end of the larva, marking its ventral and dorsal halves (Fig. 2i). This was made clearly visible by red pigment cells that were associated with the ciliated band. The ciliated band also looped ventrally to run along the ventral ridge, forming a complete and continuous loop similar to that formed in the early stages of embryogenesis in other ophioplutei (Fig. 2h, i). Although the larvae had this continuous ciliated band, a characteristic of ophioplutei, pluteal arms were not formed (Fig. 2i).



**Figure 2.** Scanning electron micrographs of the early events of development in *Ophionereis schayeri*. (a) Two-cell embryo. (b) Offset cleavage planes and asynchronous cleavage results in blastomeres of different sizes. (c) Wrinkled blastula with shallow wrinkled depressions (arrow). (d) Cracked open blastula with hollow blastocoel and ciliated epithelial cells. (e) Uniformly ciliated gastrula with vegetal blastopore (arrow). (f) Gastrula epithelium showing columnar cells with visible lipid droplets (arrowhead) and round cells (arrow). (g) Elongate gastrula with closed blastopore (arrow) and anterior stomodeal depression. (h) Early larva with a continuous ciliated band (arrowheads). (i) Side view of an early larva showing the prominent ventral ridge and the ciliated band (arrowheads) that bisects the larva into dorsal and ventral halves. Blastocoel, BL; cilia, C; dorsal, D; fertilization membrane, FM; stomodeal depression, S; ventral, V; ventral ridge, VR. Scale bars for a-e, g-i = 50  $\mu\text{m}$ . Scale bar for f = 10  $\mu\text{m}$ .

*Larval skeleton.* The bilateral larval skeleton first became evident in gastrulae as two birefringent spots on either side of the blastopore (Fig. 4a). As the gastrulae elongated, the skeleton quickly developed into a tetradial form (Fig. 4b). The rods reached their maximum length 42 h after fertilization, when the larvae had developed the ventral

ridge and ciliated band. The rods of the tetradial larval skeleton formed simultaneously, and consisted of the posterior body rods ( $\bar{x}$  = 52  $\mu\text{m}$  length, SE = 7  $\mu\text{m}$ , range: 37-93  $\mu\text{m}$ ,  $n$  = 7), which anchored the three reduced larval arm rods. The posterolateral rods ( $\bar{x}$  = 30  $\mu\text{m}$ , SE = 4  $\mu\text{m}$ , range: 18-46  $\mu\text{m}$ ,  $n$  = 7) projected in the same plane as the



**Figure 3.** Serial semithin sections through a 28-h-old larva of *Ophionereis schayeri*. Sections are oriented with the animal, or anterior, end towards the top of the figure, and vegetal, or posterior, end towards the bottom. (a) The stomodeum opens on the ventral surface. (b) The larval digestive tract is bipartite, consisting of an esophagus that is separated from the stomach by what appears to be an esophageal sphincter (arrow). (c) The gut is transiently open posteriorly via the blastopore. The gut is filled with mesenchyme cells (arrowhead). Blastopore, B; dorsal, D; esophagus, O; stomodeum, S; stomach, ST; ventral, V. Scale bars = 50  $\mu\text{m}$ .

body rods. The other two arm rods, the anterolateral and postoral rods, were approximately equal in length ( $\bar{x}$  = 25  $\mu\text{m}$ , SE = 3  $\mu\text{m}$ , range: 12–36  $\mu\text{m}$ ,  $n$  = 9) (Fig. 4c). The posterodorsal rods of typical ophioplutei never developed in the larvae of *Ophionereis schayeri*. Subsequent development resulted in the skeletal rods all developing thorns simultaneously (Fig. 4d, e).

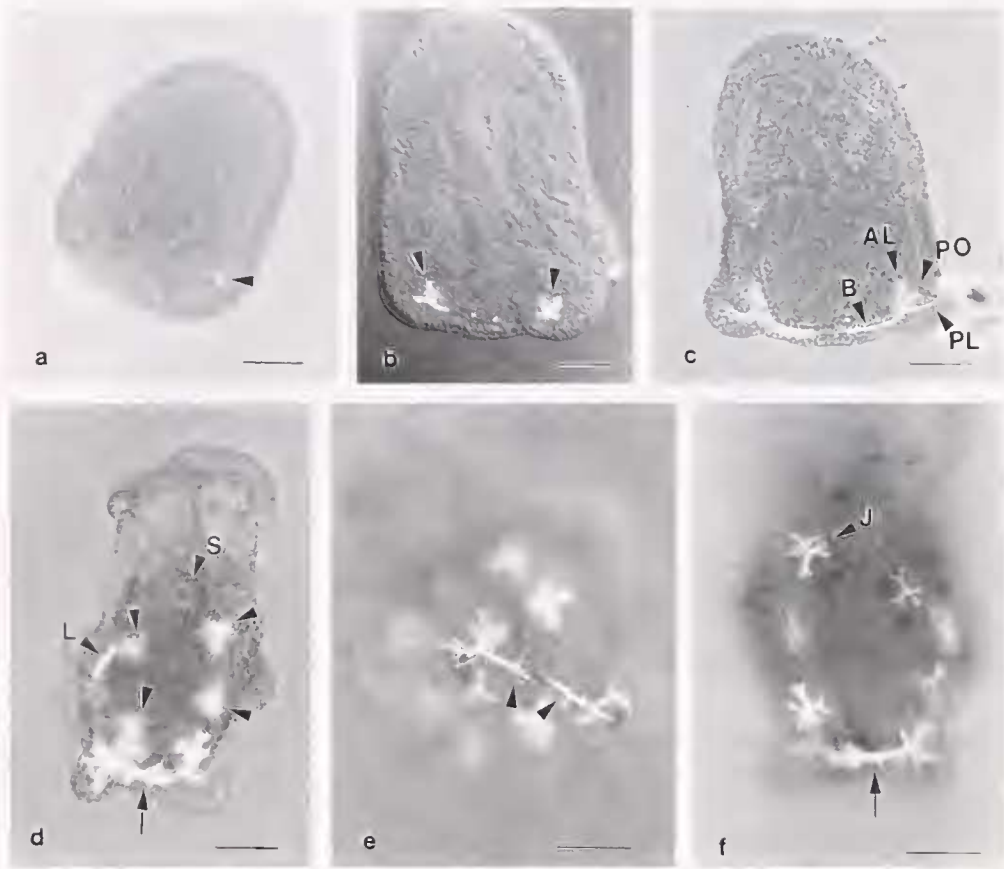
With onset of rudiment formation in the midventral region of the larva, 48–60 h after fertilization, the two body rods grew and met midway at the posterior end of the larva to form what appeared to be a continuous rod (Fig. 4d, f). The apparent joining of the two posterior body rods did not, however, seem to be accompanied by the presence of transverse or end rods, as in typical ophioplutei. Simultaneously, the adult skeleton appeared as six small birefringent spicules in the rudiment, corresponding to the central and five radial plates of the juvenile dorsal skeleton (Fig. 4d, e, f). The larval skeleton started to break up as the rudiment formed, and pieces of the larval rods migrated into the rudiment and could no longer be traced by polarized light (Fig. 4d). The adult skeletal spicules were very different from the larval skeleton. They had the multirayed shape typical of the early juvenile skeleton, and they occurred as plates rather than rods (Fig. 4e, f).

### Discussion

The larva of *Ophionereis schayeri*, although non-feeding, appears to be in an intermediate stage of evolution, since it has features characteristic of both planktrophic (ophiopluteal) and lecithotrophic development. Its ophiopluteal features include the vestigial larval skeleton, continuous cili-

ated band, and transiently complete larval gut. The non-pluteal features include a simple barrel-like shape and nonfunctional gut. The presence of vestigial larval structures in this lecithotrophic larva is evidence that the ancestral form had a feeding ophiopluteus. Ophiuroids with planktrophic larvae typically have small (80–185  $\mu\text{m}$ ) eggs (Hendler, 1991; Sewell and Young, 1997). Acquisition of a larger egg in *O. schayeri* was probably a preadaptation for the evolution of non-feeding development, with subsequent loss of superfluous larval structures. This sequence of evolutionary changes is similar to the evolution of non-feeding development in echinoids with large eggs, where loss of pluteal arms and acquisition of a simple larval shape also occurs (Olson *et al.*, 1993; Wray, 1996).

The ciliated band in *Ophionereis schayeri* larvae is a reduced expression of the continuous ciliated band typical of ophioplutei, similar to that seen in the brooded lecithotrophic larvae of *Ophionotus hexactis* (Mortensen, 1921). By contrast, its congener, *Ophionereis annulata*, has an early barrel-shaped larva that is uniformly ciliated, with no vestige of a ciliated band (Hendler, 1982). A continuous band is characteristic of feeding echinoderm larvae and is considered to reflect not only the functional requirements of feeding and swimming, but also selective pressures for a particular feeding clearance mechanism (Strathmann, 1974). Retention of a ciliated band by the non-feeding larvae of *O. schayeri* is similar to the reduction of the ciliated band in the non-feeding larvae of some echinoids (Olson *et al.*, 1993; Emler, 1995). Like the larvae of *O. schayeri*, the brooded larvae of *O. hexactis* have a digestive tract consisting of a stomodeum, esophagus, and stomach.



**Figure 4.** Cross-polarized light micrographs showing larval skeletogenesis in *Ophionereis schayeri*. (a) Gastrula with first appearance of a larval spicule (arrowhead); the other spicule is not in the plane of focus. (b) Early formation of the tetraradiate bilateral larval skeleton (arrowheads). (c) An early larva with tetraradiate skeleton consisting of anchoring posterior body rods and three arms rods—posterolaterals, anterolaterals, and postorals. (d) Rudiment formation and appearance of juvenile plates (4 unlabeled arrowheads). The two larval body rods meet midway at the posterior of the larva and seem to become continuous (arrow). The larval skeleton is thorny, starts to break up, and migrates into the rudiment. (e) Larva viewed from the posterior, showing bilateral thorny larval rods (arrowheads), with juvenile plates out of focus in the background. (f) Larva with larval skeleton still present and well-formed juvenile plates. A multirayed shape is typical of juvenile echinoderm plates. Anterolateral rods, AL; body rods, B; juvenile plates, J; larval skeleton, L; posterolateral rods, PL; postoral rods, PO; and stomodeal depression, S. Scale bars = 50  $\mu$ m.

In contrast to *O. schayeri*, however, these larvae lack an anus (Mortensen, 1921). A transiently complete digestive tract, as seen in the larvae of *O. schayeri*, apparently has not been previously reported for other lecithotrophic echinoderm larvae.

The skeletal rods in *Ophionereis schayeri* larvae are considerably smaller than those of planktotrophic ophioplutei (Mortensen, 1921), and they do not support pluteal arms. Moreover, all four rods—body, posterolateral, anterolateral, and postoral—formed simultaneously, and developed their thorns simultaneously. This contrasts with typical ophioplutei, in which the body rod, posterolateral rod, and anterolateral rod develop prior to the postoral and posterodorsal rods (MacBride, 1907; Narasimhamurti, 1933; Olsen, 1942; Mladenov, 1985). In addition, the thorns on the rods of ophioplutei do not form at the same time (MacBride, 1907;

Mortensen, 1921; Narasimhamurti, 1933; Olsen, 1942; Mladenov, 1985). Accelerated rod formation into a tetraradiate configuration shows that a heterochrony in skeletogenesis has occurred in the evolution of development in *O. schayeri*. A similar pattern of skeletogenesis is reported for the lecithotrophic larvae of *Amphiura chiajei* (Fenaux, 1963) and *Amphiopus abditus* (Hendler, 1978), and for the planktotrophic, 8-armed ophioplutei of *Amphipholis kochii*, which undergo rapid development (Yamashita, 1985). Accelerated skeletogenesis may be a mechanism to reduce the time to metamorphosis during the evolution of lecithotrophy. The skeleton is further reduced in the lecithotrophic larvae of *Ophiothrix oerstedii* and *Ophionereis annulata*, which form only three distinct skeletal rods (Mladenov, 1979; Hendler, 1982).

Posterodorsal arm rods, the last to be formed in typical

ophioplutei, are not present in *Ophionereis schayeri* larvae, or in other ophiuroid larvae with a vestigial skeleton (Mortensen, 1921, 1933; Fell, 1945; Fenaux, 1963; Mladenov, 1979; Hendler, 1982). This suggests a potential sequence of morphogenetic change, with those functionally related larval structures (e.g., pluteal arms, skeletal rods) that are formed late in planktotrophic development being the first to be lost in the evolution of lecithotrophic development. This kind of incremental loss, as depicted in Fell's (1945) diagrammatic series of ophiuroid larvae with a decreasing number of arms and shorter developmental times, is considered to be an important mechanism of evolutionary change (Anderson, 1987; Raff, 1996). The evolution of lecithotrophy in *O. schayeri* has involved reduction of several larval structures, including the skeletal rods, ciliated band, and gut, whose development is unlikely to be genetically linked. Reduction in these larval structures may have occurred independently in response to similar selective pressures.

The brooded larvae of *Ophionotus hexactis* are similar to the larvae of *Ophionereis schayeri* with respect to the form of the ciliated band, the presence of a partially developed digestive tract, and some skeletal rods (Mortensen, 1921). Similarly, the brooded larvae of *Amphipholis squamata* and *A. japonica* and the benthic embryos of *Amphioplus abditus* have a reduced larval skeleton (Murakami, 1940; Fell, 1946; Hendler, 1978). These findings show that phylogenetically diverse ophiuroids with a range of developmental modes have retained vestiges of an ancestral feeding state. Other species with lecithotrophic development, however, show no ophiopluteal features (Table 1). The evolution to lecithotrophy in ophiuroids has involved the reduction and loss of a suite of ophiopluteal structures, resulting in an increasingly simple larval form and accelerated development. Similarly, in echinoids, reducing the time to metamorphosis during the evolution of lecithotrophy involved complex developmental processes, resulting in a variety of morphological changes including loss of pluteal arms (Wray, 1996).

This study demonstrates that the internal events of development in what appear, externally, to be relatively simple lecithotrophic larvae warrant careful examination. Detection of the larval gut and skeleton in the larvae of *Ophionereis schayeri* provided important information on the extent of evolutionary change in development. A larval skeleton will be easily missed if it is dissolved by fixatives and storing buffers. Most important for ophiuroids, the discovery of larval rods in vitellariae demonstrated that this larval form evolved from an ophiopluteal ancestor (Mortensen, 1938; Hendler, 1982) and is not divergent, as previously thought (Fell, 1945). Similarly, the discovery of larval rods in the larvae of *Asthenosoma ijimai* and *Helicidaris erythrogramma* led to a reinterpretation of the extent of developmental change in these echinoids (Amemiya and Emler, 1992; Emler, 1995).

Within the genus *Ophionereis*, *O. schayeri* is the fifth species known to have lecithotrophic development (Table 1). Like *O. schayeri*, *O. squamulosa* and *O. amulata* have planktonic larvae (Mortensen, 1921; Hendler, 1982), whereas *O. vivipara* and *O. olivacea* have brooded larvae (Mortensen, 1933; Byrne, 1991). Only one species, *O. fasciata*, is known to have planktotrophic development (Selvakumaraswamy, unpubl. data), and thus most likely possesses the ancestral larval form for the genus. The relatively complete set of larval structures in the non-feeding larvae of *O. schayeri* (continuous ciliated band, tetradiate skeleton, and transiently complete larval gut), indicates it may be the most recent member of the genus to have evolved lecithotrophy. Based on morphology, *O. amulata* might be expected to be next in this evolutionary progression, because it has retained only a triradial skeleton. *O. squamulosa* would be expected next as it has a stomodeum and vestiges of the ciliated band. The extreme end of the morphological continuum would be illustrated by *O. olivacea* and *O. vivipara*, which completely lack larval structures. Non-feeding development thus appears to be common in this clade. A molecular approach is needed to determine whether the switch to lecithotrophy in *O. schayeri* was a single event or a multiple one as demonstrated for the sea star genus *Patriella* (Hart et al., 1997). The causes of selection for a particular mode of development in certain lineages are still relatively unknown, but they seem to be more prevalent in some echinoderm lineages than others (Pearse and Bosch, 1994; Byrne and Cerra, 1996).

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